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Variation in movement: multiple locomotor gaits in Neotropical harvestmen

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Navigation of complex environments is crucial for animals to find food, mates and/or shelter and to escape enemies. In order to move successfully in variable conditions, many animals have evolved the ability to switch between several patterns of locomotion or gaits. Here, we describe and differentiate between putative locomotor gaits in the harvestman, an arachnid that uses a hexapod-like alternate tripod gait. We recorded Neotropical harvestmen of the genus *Prionostemma* moving across a flat surface using high-speed video. We reconstructed three-dimensional trajectories and associated kinematics and found four different locomotor gaits: running, stotting, bobbing and walking. Gaits differed in their performance and postural kinematics, body trajectory, gait diagrams and/or kinetic and potential energy exchange. Our approach points out the importance of using multiple kinematic features to differentiate gaits. The use of a specific gait was not predicted by leg length, body area or sex. We propose testable hypotheses regarding the function of each gait and the factors that drive the evolution of different gaits. Ultimately, the diversity of locomotory gaits can allow animals to respond to different environmental challenges and contexts.

ADDITIONAL KEYWORDS: biomechanics – harvestman– kinematics – movement – Opiliones.

INTRODUCTION

Locomotion is a crucial component of the biology of a species that allows individuals to escape predators, find shelter, migrate and encounter mates. During its lifetime, an animal will move in multiple contexts and through diverse micro-environments. In order to respond to such variable contexts, many animals have evolved different ways of moving that enhance stability, manoeuvrability and performance (Dickinson *et al.*, 2000). For example, the same animal can run on the ground to escape predators and climb to reach arboreal food resources (Dagg, 1973).

A locomotor gait is a repeated pattern or sequence of body and/or limb movement that allows animals to move (Vogel, 2003; Biewener & Patek, 2018). For animals moving on land, limbs contact the substrate ('stance phase') and exchange kinetic and potential energy. Variation in the timing and duration of the stance phase and variation in the overall movement pattern of all the limbs relative to the body mediate locomotion and energetics (Sensenig & Shultz, 2006; Spence, *et al.* 2010). By varying the stance phase, performance (e.g. velocity, acceleration) and other kinematic features (e.g. stride frequency, period, stride length; Herreid & Full, 1986; Noah *et al.*, 2004; Wilshin *et al.*, 2018), an animal produces different gaits. The exchange of kinetic and potential energy is also used to define gaits (Vogel, 2003). For example, for bipedal primates, 'walking' gaits are defined by the exchanges of kinetic and potential energy that are out of phase. 'Running' gaits are defined as those in which kinetic and potential energy are in phase. For some animals (e.g. humans and some quadrupedal mammals), running gaits include a period during which both legs are off the ground ('true aerial phase'). However, for animals with a larger number of limbs (e.g. cockroaches, spiders) or of larger body size (e.g. elephants) there is no aerial phase when running (Full & Tu, 1990; Hutchinson *et al.*, 2003; Weihmann, 2013).

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The use of a specific gait is attributable to an interaction of several factors. Some of these are intrinsic to an animal, such as body size, limb length and/or number of limbs (Heglund *et al.*, 1974; Vogel, 2003; Moya-Laraño *et al.*, 2009). Gaits may also be influenced by body condition (Miller *et al.*, 1987; van Berkum *et al.*, 1989; Jakob *et al.*, 1996), which might reflect an animal's hunger level, ontogenetic and/or reproductive stage, parasite load or disease. Extrinsic factors can also modulate which gait an animal uses, including the medium in which the animal moves (air, water or a solid substrate), the physical and three-dimensional (3D) properties of that medium (Spagna *et al.*, 2007; Sponberg & Full, 2008; Spence *et al.*, 2010) and the ecological context or stimulus (FitzGibbon, 1993; Moore *et al.*, 2017; Wheatley *et al.*, 2018). For example, escape from predators and performance of courtship displays often involve different locomotory gaits (Caro, 1986).

Having more than one gait is common. For example, ghost crabs use three gaits: walking and two types of running gaits (Blickhan & Full, 1987). When moving underwater, rock crabs use an additional gait (punting), in which they alternate contacting the substrate and gliding (Martinez *et al.*, 1998). Penguins use either a walking or a 'waddling' gait when moving on land (Griffin & Kram, 2000). Quadrupedal mammals can perform a variety of gaits, such as walking, trotting, running, racking, cantering, hopping, galloping, bounding and stotting (Caro, 1986; McGowan & Collins, 2018). Insects and spiders also show extensive variation in their locomotor patterns (Ting *et al.*, 1994; Spagna & Peattie, 2012; Weihmann, 2013; Wilshin *et al.*, 2018), although their gaits have not been as thoroughly described.

Here, we studied variation in the locomotor patterns of harvestmen. These arachnids have eight long and slender legs, which is an unusual morphology in terrestrial environments. Harvestmen move across many substrates, including rock, soil, leaf litter, tree bark and foliage (Wade *et al.*, 2011; Proud *et al.*, 2012; Smith *et al.*, 2012; Domínguez *et al.*, 2016), and across a variety of different slopes. While running, harvestmen use a hexapod-like alternate tripod gait that is more similar to terrestrial insects than to some arachnids (Full & Tu, 1990; Seipel *et al.*, 2004; Sensenig & Shultz, 2006; Moya-Laraño *et al.*, 2008; Mongeau *et al.*, 2012; Wilshin *et al.*, 2018). Harvestmen do not use the second pair of legs (legs 2) to move, but instead use them as sensory appendages (but see Willemart *et al.*, 2009). In the harvestman *Leiobunum vittatum*, Sensenig & Shultz (2006) showed that kinetic and potential energy were mostly in phase during running and that their body undergoes vertical and transverse oscillations (Sensenig & Shultz, 2006). Additionally, our field observations of the Neotropical genus *Prionostemma* Pocock, 1903 (Opiliones: Sclerosomatidae) suggest that harvestmen use multiple gait types in addition to running.

By using high-speed videography, we aimed to examine locomotion in *Prionostemma* harvestmen. When moving on horizontal surfaces, we found evidence for four different gaits: running, stotting, bobbing and walking. Gaits differed in their kinematics, body trajectory, gait diagram and overall kinetic and/or potential energy exchange. We also tested whether gaits varied in relationship to morphological features. We propose hypotheses as to how ecological and morphological factors promote the evolution of gait diversity in these and other animals.

MATERIAL AND METHODS

Study animals

This research was conducted in the Neotropical lowland rainforest at La Selva Biological Station, Costa Rica (10°26′N, 84°00′W, 50 m elevation), during June–August 2015. We studied harvestmen belonging to a currently undescribed species in the genus *Prionostemma* (Opiliones: Sclerosomatidae). Previous work referred to this species as *P.* sp1. (Wade *et al.*, 2011; Grether *et al.*, 2014). All 177 adult individuals collected were of these same species. We collected only eight-legged individuals. Once collected, we placed them in clear plastic deli containers (15 cm × 12 cm × 10 cm). Animals were housed for 24 ± 4 h before running trials, during which they were fed ad libitum quantities of cucumber, apple and wet cat food.

Experimental set-up

We conducted our experiments with horizontally moving harvestmen during the daytime (from 10.00 to 15.00 h). All trials were conducted on a 60 cm track lined with white bond paper (Fig. 1; Supporting Information, Video S1). We used a GoPro camera (HERO 4 Edition; GoPro, San Mateo, CA, USA) recording at 120 frames/s, with a resolution of 1280 × 960 pixels. The camera provided a lateral view of the animals. A mirror was placed at 45° in relationship to the horizontal plane to provide an additional dorsal view. From these dorsal and lateral views, we reconstructed 3D trajectories of animal movement. For calibration, a 2 cm square was drawn in the centre of the track, and a 3 cm × 3 cm × 5 cm rectangular vial was placed in the centre of the track (Fig. 1).

To begin each trial, an individual was placed at the starting point of the track (Fig. 1). The animal was held by both hindlegs, with its forelegs (legs 1) touching the surface of the track. The animal was then released and

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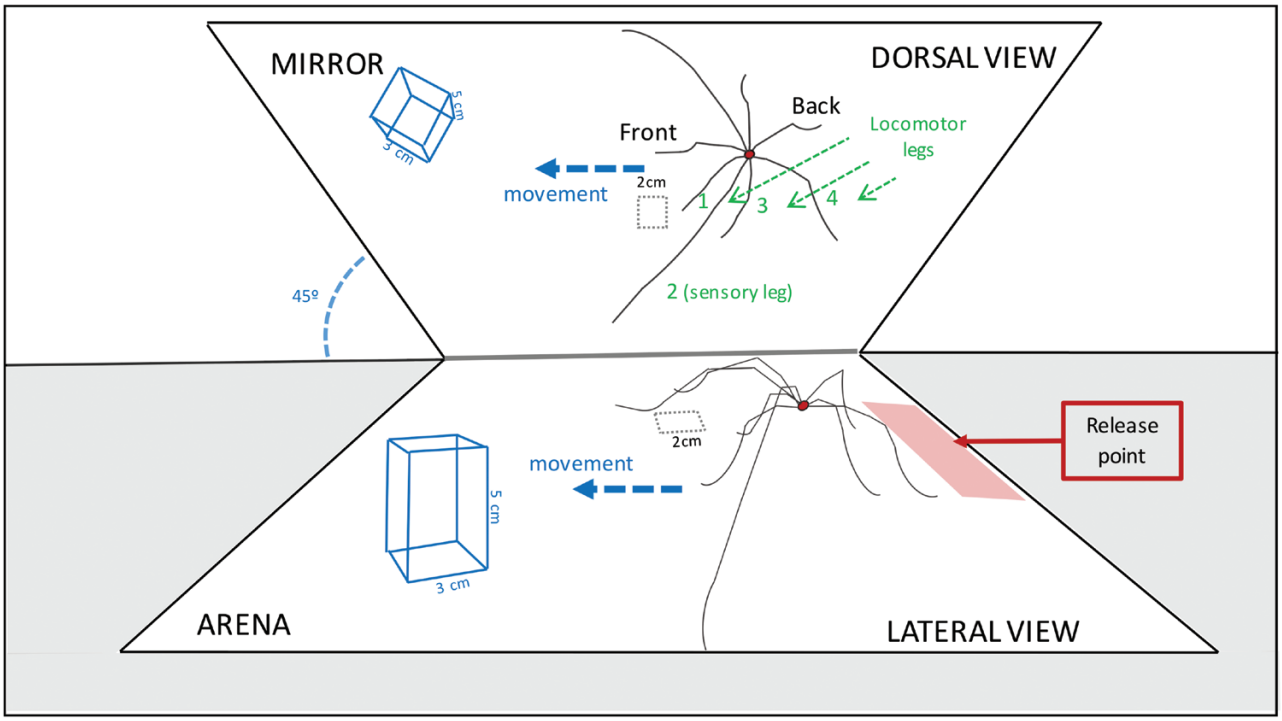

Figure 1. Set-up for the locomotor trials of *Prionostemma* sp. 1 harvestmen. The upper half is the view from the mirror placed at 45°. The camera was located in the centre of the lower side of the figure, in lateral view. The 2 cm square and the 3 cm × 5 cm vial were used to calibrate the videos (see Material and Methods). The harvestman body (red) was the centre of mass, and the focal leg tracked for the analysis was the left leg 1. The leg pair number and the leg type are shown for the harvestman in dorsal view. The release point where the trial started is shown in the right side of the arena, and the trajectory of the animal was reconstructed as it moved towards the left (dashed blue arrow), until its body left the arena. Harvestmen are shown at ×2 scale.

its behaviour recorded as it moved along the length of the track. The trials continued until the animal had reached the far end of the track. Only one trial was conducted per animal.

Video analyses

To quantify locomotion, we measured the kinematics of locomotion for each video. We first identified the first and last frames where the harvestman's body was distinguishable from the background while moving across the arena (in both lateral and dorsal views) and set these as the beginning and end of the trial, respectively. Videos were then digitized using Mathematica (v.10.4; Wolfram Research, Inc., Champaign, IL, USA). Using custom scripts, we automatically tracked the position of the animal's body using the dorsal and lateral views in each video. We first subtracted the background and then performed thresholding to obtain a binary image. We eliminated patches that were too small or large to be harvestmen, and then found the centroid of the remaining patches. Tracking errors were eliminated using a 3D reprojection error threshold. To correct for lens distortion produced by the GoPro camera, calibration parameters were obtained using a checkerboard calibration procedure in MATLAB (v.R2016a; The Mathworks, Natick, MA, USA). All digitized points were undistorted before further processing.

We reconstructed the 3D trajectory of the body of each individual (red in Fig. 1). All animals were assumed to run in a straight trajectory. Following Sensenig & Shultz (2006), we assumed that the position of the centre of mass (CoM) of the animal was approximated by the body alone and ignored changes associated with leg motions. We used the M-estimator sample consensus algorithm (Torr & Zisserman, 2000) via built-in functions (i.e. estimateFundamentalMatrix and triangulate) and tools developed by Hedrick (2008) for MATLAB. The M-estimator algorithm obtains the relative orientation and translation between the two cameras, which are used to triangulate a 3D point from the two-dimensional image coordinates from each view. For each video, the resulting *xyz* coordinates were rotated so that a vector normal to the plane was defined by the reconstructed corners of the calibration

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square and the vial. The videos were aligned and scaled so that the mean distance between all adjacent corners of the calibration square was 2.0 cm. The locations of corners of the calibration square and vial were manually digitized in both views of each video. Finally, rotated and scaled trajectories were imported into Mathematica, where we extracted kinematic and temporal data from each video. Specifically, a quintic smoothing spline [$x(t)$, which has a continuous and differentiable second derivative] was fitted to body position data vs. time for each spatial dimension. Estimated velocity [$v(t)$] and acceleration [$a(t)$] vectors were extracted from the first and second derivatives of the spline, respectively. These methods gave us measurements with an average re-projection error of 3.6 pixels.

We estimated values for 11 variables that described variation in harvestman locomotion. These included stride (variables 1–4), postural (variables 5–8) and performance (variables 10 and 11) kinematic variables. To calculate stride kinematics, we visually tracked a focal leg (typically left leg I) and noted the time when the leg touched the ground, when it was lifted,and when it touched the ground again (one stride). We calculated average kinematics over three strides. Next, we calculated: (1) duty factor, as the proportion of time during each stride that the focal leg was on the ground; (2) stride frequency, as the number of complete strides per unit of time; (3) stride period, as the time to complete one stride; and (4) stride length, as the maximal distance along the x-axis that the focal leg moved in one stride.

Using the CoM, we calculated several postural variables, specifically (5) the 3D sinuosity normalized by time. Sinuosity of a trajectory is a unitless measurement, defined as the total path length of the trajectory divided by the linear distance between the endpoints, and quantifies the degree of lateral and vertical deviation from a straight path. We also measured: (6) the minimal height; (7) the maximal height; (8) the height range during each trial; and (9) the number of times the CoM touched the ground divided by the total distance moved. For performance metrics, we included: (10) the average horizontal velocity [$\bar{v}_{\mathrm{h}} = (x_{\mathrm{final}} - x_{\mathrm{initial}})/(t_{\mathrm{final}} - t_{\mathrm{initial}})$ where x_{initial} and x_{final} are (x, y) coordinates of body position at the start (t_{initial}) and end (t_{final}) of the trial, respectively]; and (11) maximal horizontal acceleration [$a_{\mathrm{h_max}} = \max_{t \in \mathrm{trial}} a_{\mathrm{h}}(t)$, where $a_{\mathrm{h}}(t)$ is the horizontal (i.e. x and y) component of the instantaneous acceleration at time t and is calculated as $a_{\mathrm{h}}(t) = \frac{d^2}{dt^2}[x_{\mathrm{h}}(t)]$]. We decided to use these two variables because they reflect biologically relevant performance metrics in the context of escaping a potential predator.

To construct gait diagrams, we followed all eight legs visually during each trial. We noted the time when each leg was on the ground (stance phase) and when it was lifted (aerial phase) and used these values to plot gait diagrams. To determine whether there was a true aerial phase, we calculated the percentage of time during the three strides per trial in which neither the left nor the right leg was on the ground. A true aerial phase occurs when all eight legs are in the air. A high percentage of this metric indicates the presence of an extended aerial phase. Additionally, we calculated the percentage of time in the stance phase for each leg (left and right) that overlapped with that for the complementary leg. A high percentage for this metric indicates that tripods overlapped extensively in the stance phase. Together, both metrics gave us a quantitative indication of the overlap (or lack thereof) between the two tripods. We also calculated the synchrony factor, following Spagna *et al.* (2011), as the proportion of frames in which all three legs in the same tripod were in the stance phase relative to the total number of frames when any of those three legs were in the stance phase, all in the same stride. We calculated these metrics for a subset of ten individuals for each gait.

To investigate the energy exchange associated with each gait, we calculated the mass-specific kinetic energy ($KE/m = ½v_{\mathrm{h}}^2$) and potential energy ($PE/m = h \times g$), where v_{h}, h and g are the horizontal component of velocity, height above the surface and gravitational acceleration, respectively. We then calculated the correlation between kinetic and potential energy over the CoM trajectory to estimate whether the two forms of energy were in or out of phase (Cavagna *et al.*, 1977; Blickhan & Full, 1987; Full & Tu, 1990).

Morphological measurements

Individuals were preserved in 70% ethanol and deposited in the Essig Museum of Entomology at the University of California, Berkeley. We measured the dorsal body area to the nearest 0.05 cm using a dissecting scope (Leica M205 FA). Additionally, using digital callipers, we measured the length of leg IV for each individual to the nearest 0.05 mm. To classify individuals as female or male, we dissected ten individuals to examine their genitalia. Females have a globous body, with a round and pointy posterior edge when examined from a dorsal view. In contrast, the body of males is squared and has a straight posterior edge.

Data analysis

Our preliminary observations suggested that *Prionostemma* harvestmen used four different gaits.

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Using the videos, we visually categorized each trial into running, stotting, bobbing or walking (Supporting Information, Video S1) via a gestalt of features including the body trajectory, the legs used to move and the timing of each stride. This partitioning resulted in the following samples sizes: running, 105 trials; stotting, 14 trials; bobbing, 26 trials; and walking, 32 trials. To test the validity of our assigned gait types, we ran a standard linear discriminant analysis using the 11 kinematic variables mentioned above and our assigned gait type as a predictor variable. This analysis was conducted using the *lda* function of the *MASS* package in R (R Core Team, 2016).

To test for differences across gaits with respect to each performance and kinematic variables, we compared the four gaits with each other using generalized linear models. To account for multiple statistical tests, we used Bonferroni corrections by dividing the α value of 0.05 by the number of tests (11), resulting in a *P*-value of 0.0045. We tested whether the mean correlation coefficient between kinetic and potential energy during the stride differed between gaits using a β regression (Cribari-neto & Zieleis, 2010) with the *betareg* package in R. To explore for the effect of morphology, we first tested whether body area and leg IV length differed between males and females using Student's unpaired *t*-tests. Next, we tested for differences in the relative use of gaits performed by males and females with a proportion χ^2 test. Finally, we examined whether the animals performing each gait differed in leg length using ANOVAs, one for each morphological predictor.

RESULTS

Kinematics

The linear discriminant analysis resulted in 88% of the trials being classified in the same category as our initial assignment, suggesting that our qualitative categories were valid (Fig. 2). For running, 92% of trials matched the assigned category, for stotting 58%, for bobbing 83% and for walking 92%. The four gaits could be distinguished based on the first two linear dimensions obtained in the linear discriminant analysis (Fig. 2).

Gaits could also be distinguished based on performance (velocity and acceleration) and postural kinematics, particularly sinuosity and stride frequency (Tables 1 and 2; Supporting Information, Fig. S1). Performance metrics (velocity and acceleration) clustered gaits into two categories: fast gaits, which included running (speed range, 12.8–54.4 cm/s) and stotting (7.6–38.8 cm/s), and slow gaits, which included bobbing (4.6–19.6 cm/s) and walking (4.5–19.6 cm/s) (Table 1; Supporting Information, Fig. S1).

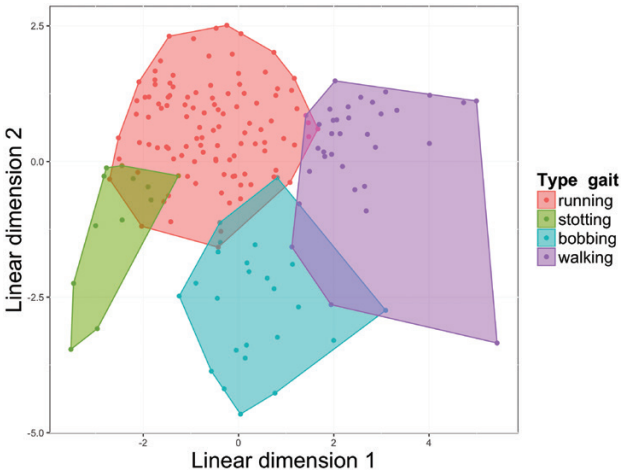

Figure 2. Linear dimensions 1 and 2 after a standard linear discriminant analysis using 11 variables to test for the ability to differentiate between different gaits in *Prionostemma* sp. 1 harvestmen.

Gait types differed in their velocity and acceleration between pairs but were indistinguishable within pairs (Table 2; Supporting Information, Fig. S1). Overall, six of the 11 kinematic variables differed between the fast and slow gait pairs. A subset of eight variables differed between fast gaits, and a different subset of five variables differed between slow gaits (Table 2; Supporting Information, Fig. S1).

Trajectory

The 3D trajectory differed among gaits (Fig. 3). Running had an overall smooth trajectory, in which the CoM had repeated vertical oscillations (Fig. 3). Stotting had a spring-like trajectory. In contrast to running, the body (CoM) of stotting individuals hit the ground at the end of every stride (Fig. 3A, B). Bobbing involved a repetitive 'bouncing' behaviour, characterized by at least two oscillations of the vertical position of the body per stride and frequent body contact with the ground (Fig. 3A, B). Walking had a less consistent trajectory, with no clear repeated movement or touches to the ground (Fig. 3A). In contrast to running, the CoM had a shorter vertical displacement during walking (Fig. 3B).

Gait diagrams

Harvestmen used six legs while performing all gaits (pairs 1, 3 and 4; for leg arrangement, see Fig. 1) and never used legs 2 (Fig. 4). While moving, harvestmen used two limb tripods alternately: legs 1R–3L–4R and legs 1L–3R–4L (R = right legs, L = left legs). When running, bobbing, and walking, legs 1R, 3L and 4R enter the stance and swing phases together and alternate

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Table 1. Kinematic variables of the four gaits performed by *Prionostemma* sp. 1 harvestmen

Site of measurement	Kinematic variables	Fast gaits								Slow gaits							
		Running (N = 107)				Stotting (N = 12)				Bobbing (N = 24)				Walking (N = 34)			
		Mean	SE	Min.	Max.	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
Centre of mass	Average horizontal velocity (cm/s)	28.14	0.83	12.81	54.40	28.00	2.33	7.59	38.78	13.62	0.87	4.56	19.64	12.67	0.58	4.53	19.58
	Maximal horizontal acceleration (cm/s^2)	13252.9	533.3	5183.0	27969.3	14457.9	1883.7	8602.5	25878.6	9713.0	1123.2	3771.1	26030.6	7351.6	568.9	2694.5	17573.2
	3D sinuosity (touches/cm)	1.38	0.04	0.51	2.95	1.88	0.08	1.50	2.33	1.05	0.04	0.60	1.43	0.63	0.03	0.21	0.98
	Body touches to the ground/ distance	0.07	0.01	0.00	0.24	0.13	0.02	0.06	0.30	0.27	0.02	0.04	0.46	0.05	0.02	0.00	0.45
	Range height (cm)	2.18	0.12	0.81	11.23	3.44	0.40	1.85	6.40	2.93	0.44	1.47	10.36	1.43	0.10	0.51	3.42
	Minimum height (cm)	0.66	0.05	0.01	1.77	0.25	0.09	0.00	1.13	0.50	0.09	0.00	1.70	1.02	0.07	0.00	1.76
	Maximal height (cm)	2.73	0.04	1.84	4.99	3.59	0.36	2.26	6.79	2.67	0.07	2.04	3.48	2.38	0.07	1.59	3.32
Focal leg	Duty factor (proportion)	0.44	0.01	0.25	0.67	0.49	0.03	0.35	0.65	0.57	0.02	0.40	0.71	0.56	0.01	0.46	0.79
	Stride frequency (Hz)	4.48	0.11	2.42	7.48	6.05	0.30	4.62	8.04	2.98	0.20	1.68	6.00	2.46	0.12	1.19	5.18
	Stride period (s)	0.24	0.01	0.14	0.41	0.18	0.01	0.13	0.22	0.37	0.02	0.17	0.63	0.44	0.02	0.23	0.84
	Stride length (cm)	6.59	0.11	3.87	9.87	5.05	0.36	2.90	7.69	4.89	0.20	3.06	6.39	5.47	0.14	4.10	7.29

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Table 2. Univariate tests for the performance and postural kinematic variables between gaits performed by *Prionostemma* sp. 1 harvestmen

Site of measurement	Kinematic variables	Does the variable differentiate…			ANOVA (all d.f. = 3,173)		
		Between pairs?	Within fast gaits? (running and stotting)	Within slow gaits? (bobbing and walking)	F	P-value	Tukey's post hoc test
Centre of mass	Average horizontal velocity (cm/s)	Yes	No	No	55.70	< 0.0001	All $P < 0.05$, except run–stot, walk–bob
	Maximal horizontal acceleration (cm/s^2)	Yes	No	No	29.89	< 0.0001	All $P < 0.05$, except run–stot, walk–bob
Focal leg	Duty factor (proportion)	Yes	No	No	34.00	< 0.0001	All $P < 0.05$, except run–stot, walk–bob
	Stride frequency (Hz)	Yes	Yes	No	58.40	< 0.0001	All $P < 0.05$, except walk–bob
	Stride period (s)	Yes	Yes	No	71.52	< 0.0001	All $P < 0.05$
	Stride length (cm)	No	Yes	No	26.20	< 0.0001	Only running compared with all $P < 0.05$
Centre of mass	3D sinuosity (touches/cm)	Yes	Yes	Yes	55.22	< 0.0001	All $P < 0.05$
	Body touches to the ground	No	Yes	Yes	50.54	< 0.0001	All $P < 0.05$, except run–walk
	Range height (cm)	Yes	No	No	10.27	< 0.0001	All $P < 0.05$, except run–bob, stot–bob
	Minimal height (cm)	No	Yes	Yes	11.57	< 0.0001	All $P < 0.05$, except run–bob, stot–bob
	Maximal height (cm)	No	Yes	No	15.51	< 0.0001	All $P < 0.05$, except run–bob, bob–walk

Central columns summarize the results from the ANOVAs presented in the right columns. Colour code: green for yes, orange for no.

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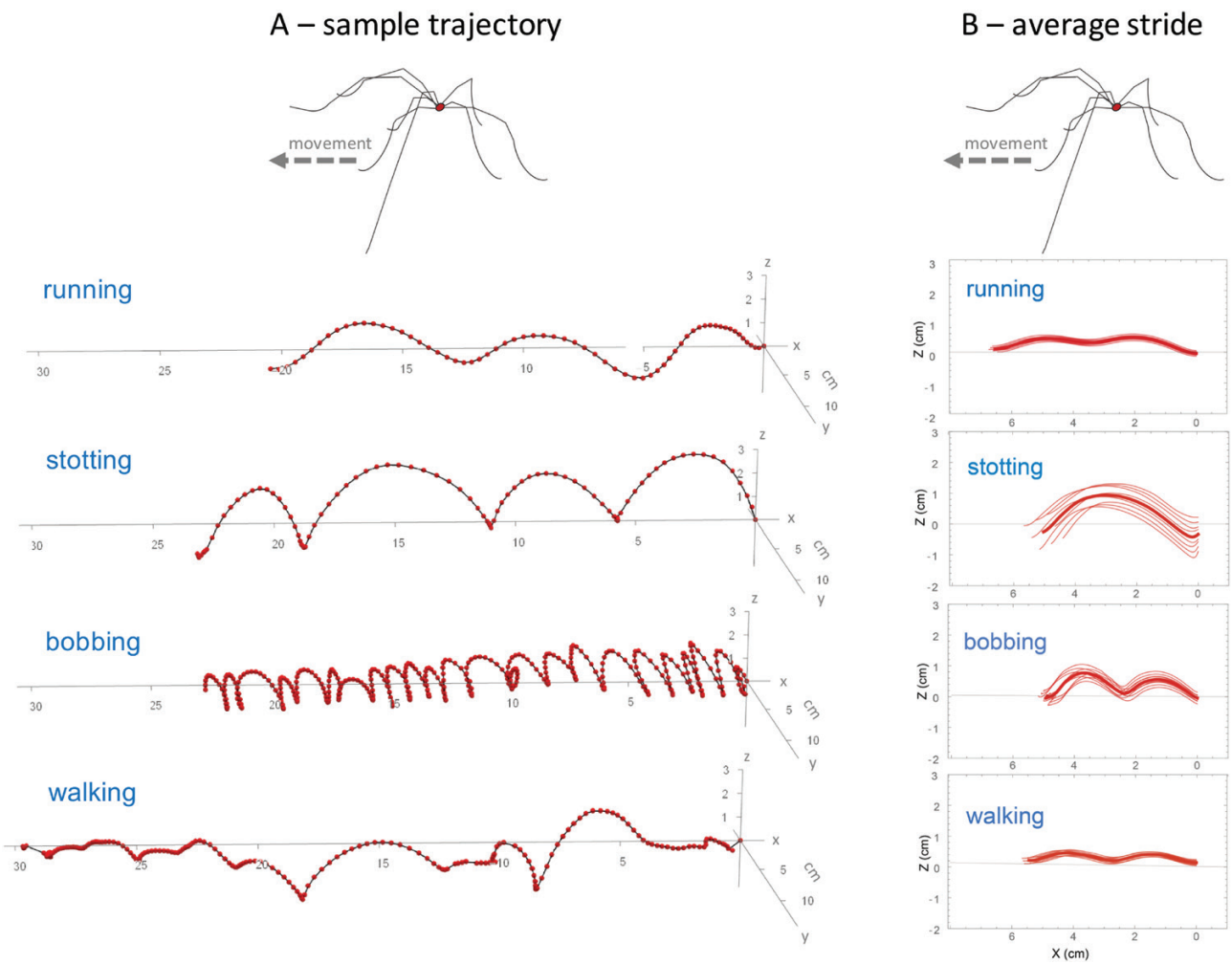

Figure 3. Body trajectories for each gait performed by *Prionostemma* sp. 1 (Opiliones: Sclerosomatidae) harvestmen. 'Movement' legend and dashed arrows represent the direction the animals moved (from right to left, as in Supporting Information, Video S1). A, sample three-dimensional trajectories for each gait. Each red sphere represents the position of the centre of mass of the animal in one frame, as tracked by our software. The black dashed line is the trajectory projected onto the *x*–*y* horizontal plane. See Material and Methods for further descriptions of the gaits. Trajectories were aligned to start in $x = 0$, $y = 0$, $z = 0$ for visual purposes, at the right side of the panel. Supporting Information, Video S1 shows the video for these trials. B, average two-dimensional (*x* and *z* planes) trajectories of a stride for each gait. Trajectories show mean (thick line) and primary modes of variation (thin lines) based on a principal components analysis constructed for this plot using the period of each reconstructed stride and *xyz* coordinates. The variation shows combinations of −1.96, 0 and 1.96 × SEM for each of the first two principal components.

with legs 1L, 3R and 4L. When stotting, however, all locomotory legs are swung forward and contact the ground simultaneously. The duty factor was lower during running (mean ± SE: 0.44 ± 0.01) and stotting (0.49 ± 0.03) than bobbing (0.57 ± 0.02) and walking (0.56 ± 0.01) ($P < 0.0001$; Tables 1 and 2; Supporting Information, Fig S1). Stride period showed the same pattern: running, 0.24 ± 0.01 s; stotting, 0.18 ± 0.01 s; bobbing, 0.37 ± 0.02 s; and walking, 0.44 ± 0.02 s ($P < 0.0001$; Table 1; Supporting Information, Fig S1). During running and stotting, each leg touched the ground for only a short period (see stride period in Supporting Information, Fig. S1). In contrast, during bobbing and walking, harvestmen left their legs on the ground for longer periods of time, resulting in a longer stance phase (Fig. 4).

A true aerial phase was observed only in stotting animals, with 30 ± 4% of the total trial time consisting of periods in which no legs were on the ground (Fig. 4). The other gaits were characterized by low percentages (running, 8 ± 2%; bobbing, 3 ± 2%; and walking, 2 ± 1%), suggesting the absence of an aerial

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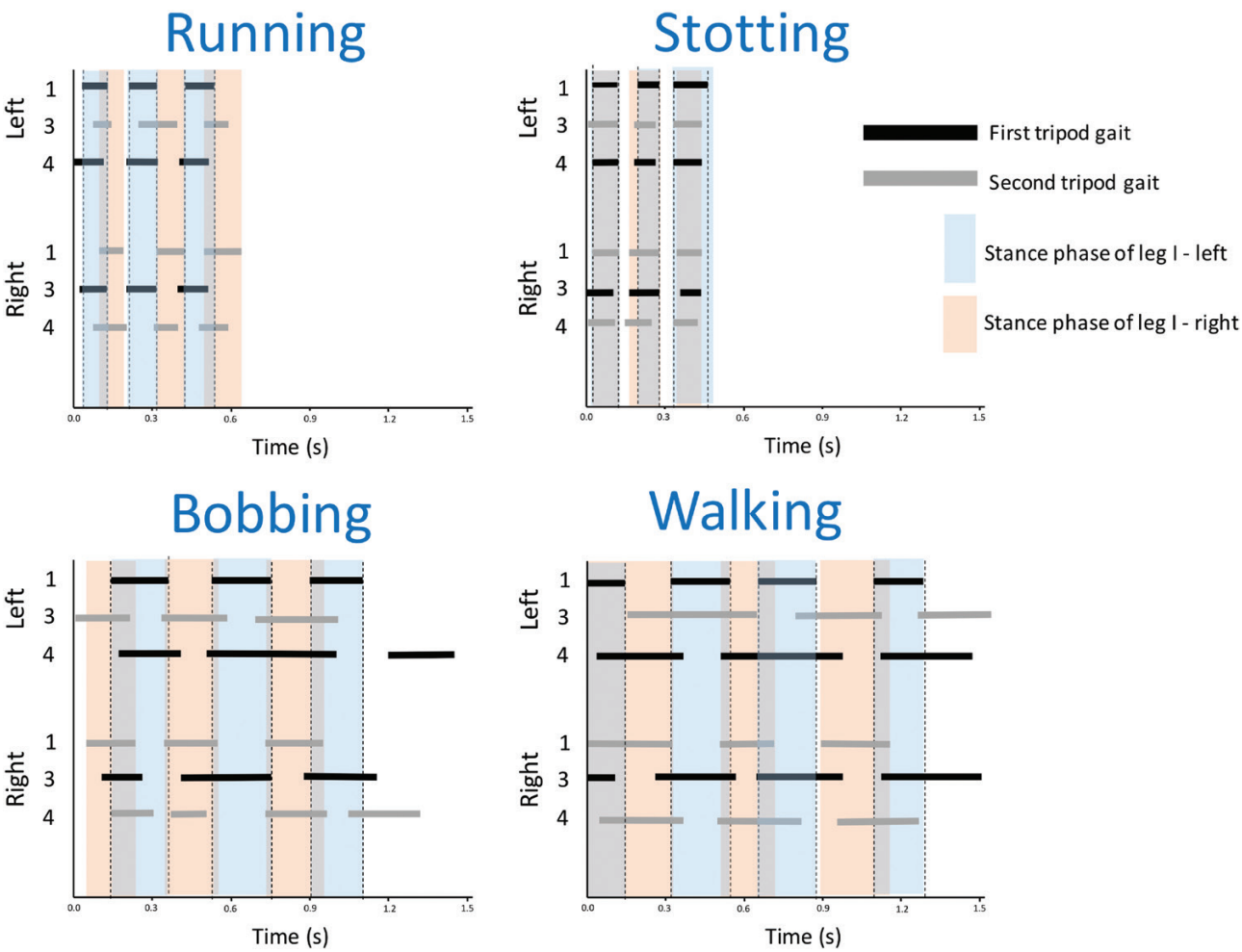

Figure 4. Representative gait diagrams of the gaits performed by *Prionostemma* sp. 1 harvestmen. Black bars represent stance phase. Bar colours mark the legs of the typical tripods used to move (black bars, 1L–3R–4L; grey bars, 1R–3L–4R; R = right legs, L = left legs). Light blue and orange shades represent the stance phase of leg 1 left and leg 1 right, respectively. The white vertical bands in the stotting panel reflect the true aerial phase, which is found only for that gait.

phase. Of the gaits with no aerial phase, walking had the highest percentage of overlap of legs 1 from the two tripods in stance phase: 97 ± 11%. Bobbing had 83 ± 12% of overlap, and running 69 ± 7% (Fig. 4). Additionally, we found that that all gaits had intermediate levels of synchrony factor between the legs of the same tripod. Those values did not differ between gaits (running, 0.40 ± 0.04; stotting, 0.40 ± 0.03; bobbing, 0.44 ± 0.07; and walking, 0.50 ± 0.06; ANOVA: $F_{3,37} = 0.83$, $P = 0.49$).

Kinetic and potential energy exchange

The kinetic and potential energy of the CoM in harvestmen seemed to be mostly in phase in running, stotting and bobbing individuals (Fig. 5A). Average correlation coefficients were positive (running, 0.50 ± 0.02; stotting, 0.57 ± 0.07; walking, 0.43 ± 0.03; bobbing, 0.60 ± 0.04; Fig. 5B), suggesting that kinetic and potential energy were in phase for these gaits. Surprisingly, kinetic and potential energy were also in phase when walking (Fig. 5A). Walking had the smallest mean coefficient of correlation between kinetic and potential energy (Fig. 5B). The β regression showed that the correlation coefficients between kinetic and potential energy differed only between stotting and walking (precision parameter phi coefficient = 5.21, $P < 0.001$; $P > 0.05$ for all other pairwise comparisons).

Morphological features

Morphology did not affect the gaits used. Legs were longer in males ($N = 98$, 68.52 ± 0.49 mm) than in females ($N = 79$, 65.16 ± 0.71 mm; $t = -3.89$, d.f. = 144.31, $P = 0.001$), although body area was

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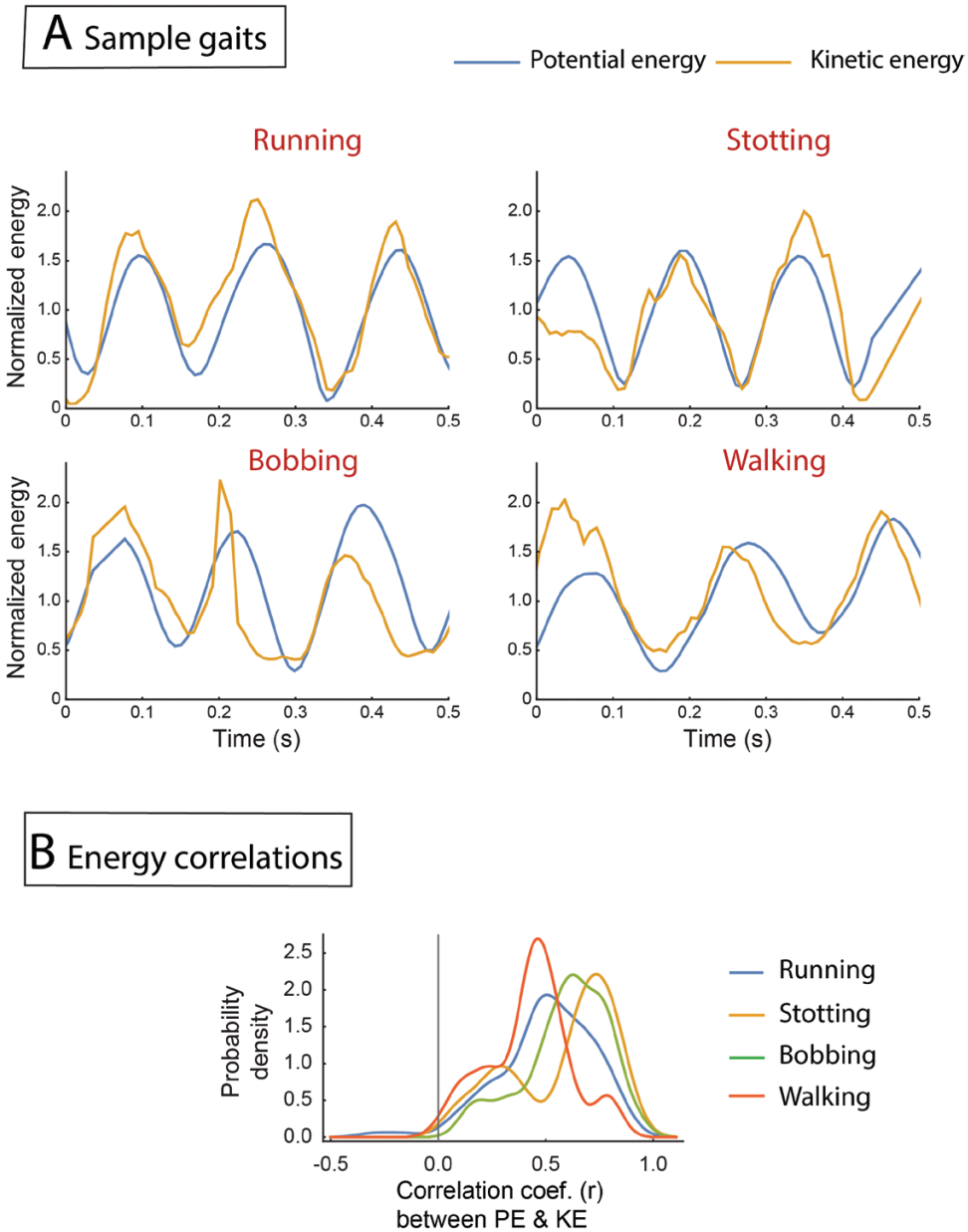

Figure 5. A, kinetic and potential energy exchange over time for the four gaits performed by *Prionostemma* sp. 1 harvestmen. Each panel represents a representative gait from the peak of the probability density of the kinetic and potential energy correlation for each gait. Supporting Information, Video S1 shows the video for these trials. B, distribution of the kinetic and potential energy correlations.

larger in females (15.46 ± 0.20 mm^2) than males (7.79 ± 0.06 mm^2; t = 36.15, d.f. = 93.862, P < 0.001; Supporting Information, Fig. S2). Females and males performed all gaits with similar frequencies (χ^2_3 = 7.41, P = 0.06; Supporting Information, Fig. S2). Finally, the type of gait performed was not predicted by body area ($F_{3,172}$ = 2.31, P = 0.08) or leg length ($F_{3,173}$ = 1.52, P = 0.21; Supporting Information, Fig. S2).

DISCUSSION

Locomotor gaits

We found that harvestmen use four distinct gaits: running, stotting, bobbing and walking. These gaits differed in a combination of postural and performance kinematics, the 3D body trajectory, gait diagrams, and kinetic and potential energy exchange (Table 3; Supporting Information, Video S1). Gaits generally

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Table 3. Distinctive features of the different gaits performed by *Prionostemma* sp. 1 harvestmen

Gait	Performance group	Distinctive kinematics	Trajectory	Gait diagrams	Use of alternating tripod gait	Potential and kinetic energy oscillations
Running	Fast	Highest stride length	Smooth trajectory; centre of mass vertical oscillations of small amplitude	Lowest overlap of tripods	Yes	In phase
Stotting	Fast	Highest stride frequency, sinuosity and maximal height; lowest period	Spring-like trajectory, starting and ending on the ground at each cycle	Only gait with real aerial phase. Legs of the same pair are on stance or aerial phase simultaneously	No	In phase
Bobbing	Slow	Highest touches per distance	Two centre of mass oscillations per stride	High overlap of tripods in stance phase	Yes	In phase
Walking	slow	Lowest sinuosity and height range	Centre of mass rarely oscillated vertically. Body rarely touched the ground	High overlap of legs in stance phase	Yes	Mostly in phase

differed along some but not all dimensions. For example, running and stotting did not differ with respect to performance (velocity or acceleration) but were different in terms of postural kinematics (i.e. sinuosity and stride frequency). The same pattern was evident between bobbing and walking. Although the linear discriminant analysis classified most gait trials according to their a priori assignment, 12% of trials were misclassified, particularly stotting gaits. This discrepancy was probably attributable to the relatively small number of trials and to overlap with the kinematics of stotting and running (Fig. 2; Table 2). Despite this, our analysis found important differences between running and stotting, specifically in the higher number of ground contacts and the presence of an aerial phase during stotting. These features suggest that stotting harvestmen have relatively high horizontal acceleration but might have reduced control over their movement during the aerial phase and suffer energetic losses from ground contacts. Overall, our approach highlights the importance of using multiple features to examine locomotion.

All our analyses assumed that locomotion followed a straight path, although this was not always the case. Similar assumptions have been made in work on other systems, and it has been noted that standard measurements (such as those included in the present study) are not affected by this assumption (Jindrich & Full, 1999). Future work, however, should test how trajectory direction affects kinematic measurements.

An extended repertoire of locomotor gaits, such as the ones we described, is unusual for terrestrial arthropods. This raises intriguing questions regarding the adaptive basis and biomechanical mechanisms underlying this variation in locomotion. Harvestmen gaits varied with respect to postural kinematics, suggesting that adjustments to duty factor, stride frequency, body contacts and/or the timing of the stance phase changed locomotion (Heglund *et al.*, 1974, Biewener & Patek, 2018). Similar results have been found for mammals (Alexander, 1989; Biewener, 1990), wolf spiders (Wilshin *et al.* 2018) and sea roaches (Kano *et al.*, 2019). These results suggest that seemingly small adjustments in kinematics can modulate locomotion.

We did not find evidence that any measured intrinsic factors predicted the gaits performed. No morphological features (leg length or body area) predicted gait type, as has been shown for other animals (Heglund *et al.*, 1974; Pontzer, 2007; Grossi *et al.*, 2016). Males and females performed gaits with similar frequency, providing evidence that sex did not influence locomotion. However, it is possible that other factors, such as body condition, energetic reserves, fatigue or experience, could predict gait use. Our experimental design controlled as many factors

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as possible, including the length of time that animals were kept in captivity, their diet, lighting, temperature and humidity. Additionally, the release stimulus was as similar as possible between individuals. Regardless, future work can explore the potential influence of other factors in the variation of gait performance.

Adaptive value of gaits

Our experimental protocol is likely to have mimicked a predation attempt on *Prionostemma* harvestmen. We thus interpreted three gaits (running, stotting and bobbing) as escape manoeuvres (Wheatley *et al.*, 2018). Stotting had high performance (velocity and acceleration), similar to running, suggesting fast escape. Stotting has also been identified as an antipredator behaviour in other animals (i.e. Thompson's gazelles; FitzGibbon, 1993). Bobbing by harvestmen had at least two oscillations of their body during each stride (Table 3), suggesting that this behaviour might disrupt the search image of visually oriented predators. An unpredictable escape trajectory, such as that observed during bobbing, can increase evasion of predators, as suggested for desert rodents (Moore *et al.*, 2017). A behaviour similar to bobbing has been observed previously in harvestmen (Holmberg *et al.*, 1984; Cockerill, 1988; Wade *et al.*, 2011; Cook *et al.*, 2013), although these descriptions did not involve forward body displacement.

In contrast to running, stotting and bobbing gaits, walking is unlikely to function as an escape manoeuvre given that walking harvestmen had lower speed and acceleration and a less sinuous trajectory compared with the other gaits. Regardless of the specific function of each gait, we suggest that having different gait types allows animals to optimize energy use (Alexander, 1989; Bertram, 2005) and ensure survival in a variety of ecological contexts. Additionally, multiple gaits might allow harvestmen the opportunity not only to escape a variety of predators, but also to lessen the likelihood that predators could learn specific strategies to catch them (Hughes, 1979; Sih, 1992).

Ecological correlates of gait variation

Natural history observations of *Prionostemma* sp. 1 harvestmen generate testable hypotheses about the contexts in which different gaits would be expected. At night-time, when harvestmen move across the ground to forage, they are frequently running or walking. Walking is common while holding food items, whereas running harvestmen seldom carry any items (I. Escalante, pers. obs.). These observations suggest that walking is performed during foraging and navigation, whereas running is not. In the field, we have observed harvestmen stotting and jumping from foliage or tree trunks after being touched, running to the underside of big leaves and retreating to crevices in trees or leaf litter. Bobbing has also been observed in the field for *Prionostemma* harvestmen, especially at night (Wade *et al.*, 2011) and when animals are touched (I. Escalante, pers. obs.). In daytime roosting aggregations (of 10–100 individuals), a tactile stimulus can elicit bobbing, which can then propagate through the group, triggering a wave of bobbing in the aggregation (I. Escalante, pers. obs.). This is similar to the defensive response of other harvestmen (Machado *et al.* 2002) and the shimmering defensive behaviour of the giant honeybee *Apis dorsata* (Kastberger *et al.*, 2014). Together, these observations support our hypothesis that running, stotting and bobbing function as predatory escape responses.

The use of different gaits might also be a response to variable energetic demands. Although we found that most gaits had kinetic and potential energy in phase, the extent of the correlation between these two measures varied. Contrary to findings for other animals (Full & Tu, 1990; Vogel, 2003), walking harvestmen did not show out-of-phase kinetic and potential energy exchange, because the correlation coefficient was, on average, greater than zero. Deviations from the expected kinetic and potential energy exchange have been found for other arthropods, such as cockroaches and spiders, during walking (Full & Tu, 1991; Weihmann, 2013). This suggests that while walking, harvestmen are not relying on pendular mechanics, and their locomotion does not follow the predictions of the inverted pendulum model (Cavagna *et al.*, 1977; Full & Koditschek, 1999; Moya-Laraño *et al.*, 2008), as found for the short-tailed opossum (Parchman, 2003). Consequently, while walking, harvestmen might be expending additional energy with each stride. In contrast, fast gaits (running and stotting) had stronger correlations, which has been suggested to favour energetic efficiency given higher speeds, because energy can be stored and recovered via skeletomuscular elastic elements in the legs (Sensenig & Shultz, 2006; Biewener & Patek, 2018). Additionally, increased body impacts during stotting probably absorbed energy and led to increased energy requirements. The gait types we identified here are only one of many aspects that must be considered to gain a full understanding of the energetics of locomotion in animals. Further work can address this by studying metabolism (for instance, oxygen consumption; Schmitz, 2005; Fleming & Bateman, 2007; Somjee *et al.*, 2018), measuring ground reaction forces of single legs (Jindrich & Full, 1999; Reinhardt & Blickhan, 2014) and modelling energy efficiency across gaits.

Diversity in gaits might also allow animals to navigate substrates that differ three-dimensionally in structure, complexity and physical properties (Spagna *et al.*, 2007;

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Sponberg & Full, 2008; Spence *et al.*, 2010). Locomotion performance can be substrate specific. For example, variation in the surface roughness of trees and liana stems was correlated with the running speed of some tropical ant species (Yanoviak *et al.*, 2017). Six-lined racerunner lizards showed substrate-specific locomotor performance, when comparing grass, sand and pebbles (Sathe & Husak, 2018). In *Prionostemma* harvestmen, individuals ran faster on soil than on smooth tree bark or mossy trees (Domínguez *et al.*, 2016). We did not test for substrate-specific gaits, but we expect that harvestmen can perform different gaits depending on the variation in substrate properties and/or the presence of physical obstacles, such as foliage, leaf litter, crevices or rocks.

Conclusion

We found that *Prionostemma* harvestmen use four different locomotor gaits: running, stotting, bobbing and walking. Gaits differed in their performance and postural kinematics, body trajectory, gait diagrams and/or kinetic and potential energy exchange. These findings point out the importance of using multiple kinematic features to differentiate gaits. We suggest that multiple factors contribute to this variation in gait observed in harvestmen during this study. These factors include variation in predator pressure, the energetic demands of different tasks (escape, foraging, mating, etc.) and the biomechanical and energetic requirements of moving through different terrain. Collectively, these factors might drive the evolution of plasticity in locomotor gaits. This plasticity, in turn, provides animals with a diverse repertoire of locomotion strategies from which they can choose in order to respond to variable and changing environmental conditions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Video S1. Locomotor gaits performed by *Prionostemma* sp. 1 harvestmen. See Material and Methods for a brief description of each gait and for the details of the video set-up. Gaits shown in this video are plotted in Figures 3 and 5.

Figure S1. Mean (± SD) values of the kinematic variables used to describe and differentiate the four gaits used by *Prionostemma* sp. 1 harvestmen. Yellow plots represent performance metrics (velocity and acceleration), green plots represent postural metrics, and purple plots are height metrics. Letter codes represent the results of Tukey's post hoc tests performed for each variable; different letters represent statistically different groups at the $P < 0.05$ level.

Figure S2. Morphological measures of *Prionostemma* sp. 1 harvestmen. Colours represent the type of gait performed, and shapes represent sex, female or male (see Results for statistical details). The inset shows a dorsal view of one female (♀) and one male (♂). Scale bar: 3 mm.

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